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MILKWEED PATCH QUALITY, ADULT POPULATION STRUCTURE, AND EGG LAYING IN THE MONARCH BUTTERFLY

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ABSTRACT. Relations between hostplant patch attributes (patch size, plant density, plant age, nectar availability), adult population structure (population size, sex ratio, age structure), and measures of egg laying (number of eggs per plant, total number of eggs per patch) in *Danaus plexippus* (L.) and its hostplant *Asclepias fruticosa* L. were investigated. Sex ratios were male biased in areas with high hostplant density (patches), and female biased in nonpatch areas. Numbers of eggs per plant were higher on single, isolated plants (areas of low hostplant density) than on patch plants. Relations between adult population attributes and measures of egg laying were not clear-cut. Contrary to expectations, neither nectar availability nor sex ratio influenced measures of egg laying. Patch size and number of females in a patch were also unrelated to total number of eggs in a patch. However the last was positively related to number of males and percentage of young females in a patch, and negatively correlated with percentage of young males in a patch.

Additional key words: *Danaus plexippus*, Nymphalidae, *Asclepias fruticosa*, Australia.

Boggs and Gilbert (1979) demonstrated that mating provides not only sperm but also nitrogen-rich nutrients for egg production by females in the monarch butterfly, *Danaus plexippus* (L.), and two heliconid species. This nutritional contribution may be most important in multi-mating species which produce large spermatophores, such as *D. plexippus* (Burns 1968, Pliske 1973, Suzuki & Zalucki 1986). Bull et al. (1985) and Suzuki and Zalucki (1986) showed experimentally that female *D. plexippus* are more likely to remain in and around patches of the milkweed *Asclepias fruticosa* (L.) where the sex ratio [males/(males and females)] is greater than 0.5. This implies that males are a major limiting resource for females.

Many factors in addition to males influence egg laying on hostplants, including species, size, age, and condition of the plants (Zalucki & Kitching 1982a). Egg laying in patches of plants is further influenced by patch size, rules of female movement (Zalucki & Kitching 1982a, 1982b, Zalucki 1983), and female age (Zalucki 1982). In this study, we looked for relations among monarch population attributes around patches (population size, sex ratio, age, and distribution), patch characteristics (size, plant density and age, nectar availability) and egg "investment" (number of eggs per plant, total number of eggs per patch), after

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TABLE 1. Effect of patch category on sex ratio (proportion male) in two sampling periods.

	Sampling period					
	24–31 Aug. 1983			20 Feb.–1 Mar. 1984		
Patch category	No. of patches	Mean ± SD sex ratio	Range of sex ratios	No. of patches	Mean ± SD sex ratio	Range of sex ratios
Nonpatch	4	0.38 ± 0.11	0.24–0.50	4[a]	0.43 ± 0.03	0.40–0.47
Small	8	0.54 ± 0.10	0.35–0.66	7	0.61 ± 0.09	0.43–0.69
Medium	1	0.63	—	4	0.65 ± 0.07	0.58–0.72
Large	2	0.46 ± 0.01	0.45–0.47	2	0.61 ± 0.08	0.55–0.67

[a] Excludes 1 misclassified nonpatch.

recording these attributes from a large and diverse sample of milkweed patches over a short duration.

MATERIALS AND METHODS

Milkweed patches were sampled on two occasions giving a total of 33 patches. During the first sampling period (24 to 31 August 1983), monarchs in and very near 15 patches were netted for 1 person h at each patch. All butterflies caught were sexed and scored for age on the basis of wing condition as follows: A′—wing soft, A—wings intact, B—wings frayed, C—wings very frayed. In this first survey, patches were classified subjectively: nonpatch (milkweed scattered and at very low density, <1 plant/m^2), small patch, medium, or large patch. Egg numbers were not recorded. This survey could be used only to ascertain relations between patch category and butterfly sex ratio. Patches were located in and near Beenleigh (27°43′S, 153°12′E), Logan Village (27°46′S, 153°06′E), and Mt. Crosby (27°32′S, 152°42′E) in SE Queensland, Australia.

On the second sampling occasion (20 February to 1 March 1984), 18 patches located along the Kenmore (27°30′S, 152°56′E)–Mt. Crosby Road were used. Adults were netted for 1 person h per patch, sexed, and aged as before. An attempt was made to estimate adult sampling efficiency. In smaller patches it is easier to obtain a high sampling fraction than in large patches. Sampling fractions were estimated subjectively on the basis of butterflies seen after netting ceased. Sampling fraction is the ratio of butterflies caught in 1 person h to butterflies caught plus those seen flying at the end of netting. Patch size was measured by idealizing the patch to standard shapes (circle, square, etc.) and recording relevant distances using a tape measure. Plant density within a patch was estimated using 6 to 25 randomly thrown 1-m^2 quadrants. From each patch a sample of ca. 100 plants was selected, cut at ground level, placed in plastic bags, and returned to the labo-

TABLE 2. Details of sampling during 20 February–1 March 1984.

Date	Starting time (h)	Temperature range (°C)	Remarks	Patch category*	Sex ratio	Sampling fraction
20-2-84	0945	21–29	Cloudy,	3	0.69	0.80
	1045		showers	2	0.69	0.80
21-2-84	0855	22–30	Cloudy,	2	0.66	0.70
	0950		fine	1	0.47	0.30
	1040			3	0.72	0.70
	1145			2	0.69	1.00
22-2-84	0910	22–27	Cloudy	2	0.56	0.70
	1000			4	0.55	0.30
	1100			3	0.61	0.80
23-2-84	0910	21–29	Cloudy,	3	0.58	0.60
	1000		showers	2	0.43	0.30
	1055			4	0.67	0.70
28-2-84	0935	22–36	Fine	2	0.67	0.30
	1015			1	0.43	0.80
	1100			2	0.67	0.60
1-3-84	0900	20–27	Cloudy	2	0.59	1.00
	0945			1	0.44	0.70
	1035			1	0.43	0.80

* 1 = nonpatch; 2 = small patch, <20,000 plants; 3 = medium patch, 20–80,000 plants; 4 = large patch, >80,000 plants.

ratory. These were measured and classified as young, with flowers, with small pods, with old pods, or dead. They were then searched for eggs and larvae. Percentage of flowering milkweed plants provided an estimate of nectar availability. Other potential nectar resources (lantana, weeds) were scored subjectively as low, medium, or high.

RESULTS

Data from both sampling periods were combined to look for relations between patch category and sex ratio (Table 1). A two-way ANOVA on an arcsin (square root) transformation (Sokal & Rohlf 1981) indicated highly significant effects of patch category ($P < 0.001$) and sampling period ($P < 0.05$). However, removing the nonpatch category from analyses removed the effects of both patch category ($P > 0.05$) and sampling period ($P > 0.05$) on sex ratio. Nonpatches had consistently female-biased sex ratios (Table 1) whereas patches, regardless of size, had variable but generally male-biased sex ratios (Table 1).

More detailed observations were made during the second sampling period. Neither time of day nor weather had any obvious effect on sex ratios or sampling fractions (Table 2). Sampling fraction is a function of patch size and terrain. Smaller sampling fractions were recorded for large patches and for patches on hillsides or with long grass.

Relations between various measures for eggs laid, patch, and butterfly

TABLE 3. Correlation matrix for all variables in 13 patches. Only coefficients significant at $P < 0.05$ are shown. * indicates significance due to one or two outlying points.

Variable label		X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11	X12	X13	X14
Patch size	X1														
Plant density	X2														
Total no. plants[a]	X3	0.87													
% flowering	X4														
Other nectar	X5														
Plant age	X6			0.50											
No. eggs/plant	X7		−0.53												
No. ♂[b]	X8	0.67	0.48	0.90			0.53	−0.55							
No. ♀[b]	X9	0.65	0.49	0.84*			0.51		0.90						
Total no.	X10	0.68	0.50	0.89*			0.53	−0.52	0.98	0.97					
Sex ratio	X11									−0.60*					
% young ♂	X12	−0.53													
% young ♀	X13							0.57*							
Total no. eggs[c]	X14	0.85		0.88					0.74*	0.68*	0.73		−0.65		

[a] (Patch size, m^2) × (no. plants/m^2).
[b] Corrected for sampling fraction.
[c] (Total no. plants) × (mean no. eggs/plant).

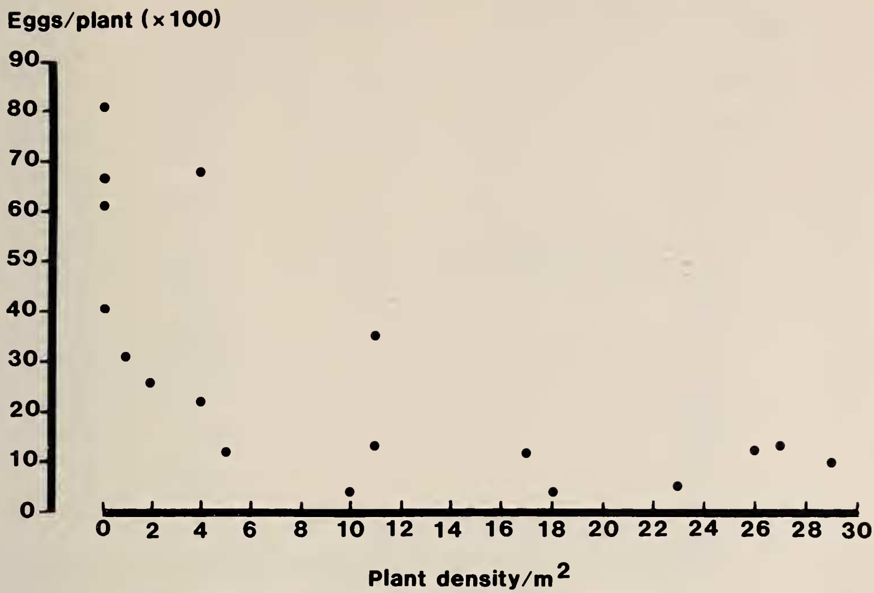

FIG. 1. Effect of plant density on number of eggs per 100 plants. Points with plant density 0 correspond to nonpatches.

variables were compared using all possible pairwise correlations, ignoring nonpatches. The correlation matrix (Table 3) shows only coefficients significant at $P < 0.05$ (one-tailed *t*-test). Some correlations were "significant" due to one or two outlying points. These relations are probably superficial.

A number of patterns are apparent in Table 3. Patch-size variables (area and total number of plants in patch) and numbers of adult butterflies were positively correlated with total numbers of eggs in patches. However, numbers of eggs per plant were negatively related to plant density (Fig. 1) and patch size. Plant age (% plants with pods and dead stems) correlated positively with numbers of butterflies, but this may follow from the positive association between total numbers of plants and plant age.

One striking result was that neither number of females nor percentage of young females in a sample had any influence on total number of eggs or number of eggs per plant, respectively, once outlying points were removed. Equations for these relations are: Total no. eggs (y) = 167 × No. females (x) + 1,775, $F_{1,11} = 9.493$, $P < 0.05$ when all points included; deleting one outlier, $y = 25x + 4{,}177$, $F_{1,10} = 0.079$, $P > 0.05$; and No. eggs/plant (y) = 0.57 × % young females (x) − 1.87, $F_{1,11} = 5.277$, $P < 0.05$ when all points included; deleting two outliers, $y = 0.091x + 10.16$, $F_{1,9} = 0.144$, $P > 0.05$).

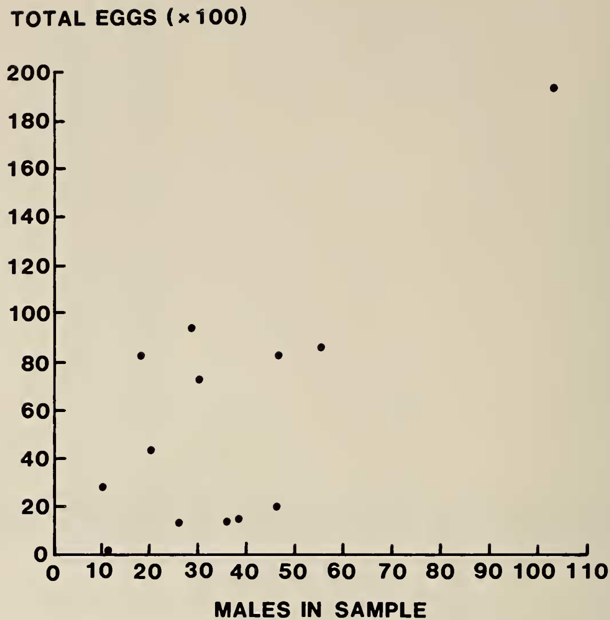

FIG. 2. Effect of number of males caught on total number of eggs in a patch.

On the other hand, number of males in a sample had a negative association with number of eggs per plant, a positive one with total number of eggs (Fig. 2), and the latter was negatively related to percentage of young males in a patch (Fig. 3). The positive association between number of males (x) and total number of eggs (y) was significant ($P < 0.05$) only if all points were included (Fig. 2, $y = 158x + 37.8$, $F_{1,11} = 13.62$). Deleting the extreme value from this figure removes significance ($y = 67.39x + 2{,}585$, $F_{1,10} = 0.8958$, $P > 0.3$). This was not the case for the relation between total number of eggs (y) and % young males (x) (Fig. 3). Removing one or two extreme values did not change this relation (with the two extreme left-hand points deleted, $y = -295.7x + 17{,}676$, $F_{1,9} = 5.728$, $P < 0.05$). The negative association of number of eggs per plant and number of males probably stems from the negative relations of number of eggs per plant to total plant number and density, and the strong positive association between these variables and male number (Table 3). Neither nectar availability nor sex ratio influenced adult numbers or measures of egg laying.

For any set of data where most variables are correlated and interdependent, single pairwise comparisons may be misleading. From the above analysis the variables total number of eggs in a patch, patch size, numbers of males and females, and percentages of young males and

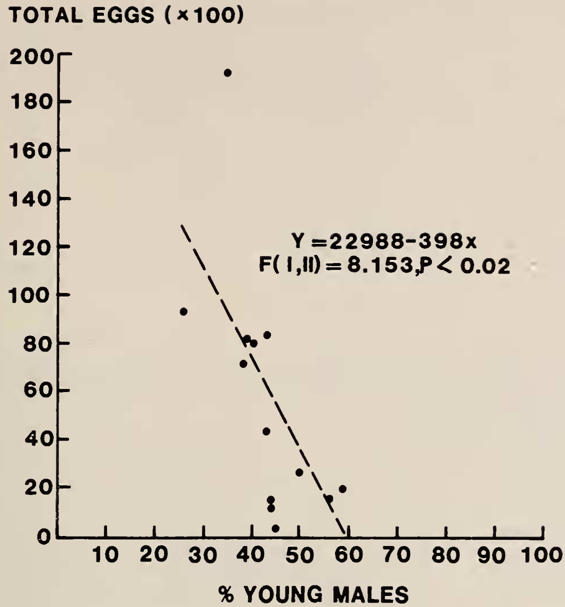

FIG. 3. Relation of percentage of young males to total number of eggs in a patch.

females in a patch were entered in a partial correlation matrix (Table 4). Total number of eggs in a patch was positively correlated with male density, but negatively correlated with percentage of young males in the population. Total number of eggs laid and percentage of young females were also positively related ($P < 0.10$), as was egg number and percentages of young males and females ($P < 0.05$). Surprisingly neither patch size nor number of females was related to total number of eggs laid.

These analyses were corroborated by stepwise linear regression with total number of eggs as the dependent variable. Results (Table 5) indicated significant effects only for number of males, % young males, and % young females.

DISCUSSION

Zalucki and Kitching (1985) and Bull et al. (1985) found that sex ratios tend to be male-biased in and around milkweed patches. If, as they suggest, male bias cannot be explained by sex ratio at birth, survival difference, or sampling bias within a patch, then where do the females go? The present study confirms male bias around milkweed patches (ca. 60%) and demonstrates a female-biased population outside patches (nonpatch areas), hilltops notwithstanding. As with many Lepidoptera

TABLE 4. Partial correlation matrix for selected patch, butterfly, and egg-laying variables.

			Number		% young	
	Total eggs X1	Patch size X2	Males X3	Females X4	Males X5	Females X6
x2	0.52					
x3	0.72**	−0.17				
x4	−0.37	0.24	0.80**			
x5	−0.79**	0.13	0.69**	−0.40		
x6	0.62*	−0.10	−0.52	0.20	0.60*	

** $P < 0.01$; * $P < 0.05$.

(Shields 1967, Parker 1978, others) male monarchs can be taken in numbers around hilltops.

The egg-laying pattern found by Zalucki and Kitching (1982a) on artificial milkweed "patches" was also confirmed by this study. Number of eggs per plant was much higher on single isolated plants than on patch plants (Fig. 1). This result can be explained in part by how female monarchs search for and use a host plant (Zalucki & Kitching 1982b, Zalucki 1983), and by female-biased sex ratios outside patches (single plants). Jones (1977) found a similar pattern of egg-laying in *Pieris rapae* (also see Shapiro 1981, Thompson & Price 1977, Wiklund & Ahrberg 1978). However, there are many alternate explanations for such a pattern (Mackay & Singer 1982).

Within patches, relations among patch and butterfly variables and measures of egg-laying are not straightforward. Contrary to expectation, sex ratio was not related to any measure of egg-laying. Nor was number of eggs in a patch related to availability of nectar, number of females in a patch, or patch size (Tables 3–5). Bull et al. (1985) and Suzuki and Zalucki (1986) showed experimentally that female residence time in a patch is positively related to sex ratio, and Bull et al. (1985) could not find any effect of butterfly density on residence time. Neither study recorded egg numbers in experimental patches.

In the present study, number of eggs in a patch was positively related to number of males (all ages), but not to number of females, even though the latter two variables are strongly positively associated (Tables 3, 4). This provides further circumstantial evidence that males are a major "egg-laying resource" for females through provision of nutrients as well as sperm at mating (Boggs & Gilbert 1979, Suzuki and Zalucki 1986). Also, Herman and Barker (1977) showed that mating stimulates oogenesis. There was a weak positive relation between female age structure and number of eggs; patches with a high percentage of young females had more eggs. This presumably reflects the high fecundity of such females (Zalucki 1982).

TABLE 5. Stepwise linear regression of total number of eggs against patch size, number of males and females, and % young males and females.

Independent variable	Coefficient (±SE)	Standardized Coefficient	t-value	P
Patch size	18.88 (11.67)	0.28	1.618	NS
No. males	153.40 (55.54)	0.72	2.762	**
No. females	−65.18 (61.35)	−0.27	−1.062	NS
% young males	−271.40 (80.34)	−0.44	−3.379	**
% young females	69.16 (33.21)	0.23	2.083	*

** $P < 0.05$; * $P < 0.10$.

In contrast, number of eggs in a patch was inversely related to percentage of young males in the population. Are young males more aggressive (inexperienced) in courtship and do they subsequently "drive" females from a patch? This hypothesis will require further testing.

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